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Global Qualitative Analysis for a Ratio-Dependent Predator–Prey Model with Delay[1]

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A ratio-dependent predator–prey model with time lag for predator is proposed and analyzed. Mathematical analyses of the model equations with regard to boundedness of solutions, nature of equilibria, permanence, and stability are analyzed. We note that for a ratio-dependent system local asymptotic stability of the positive steady state does not even guarantee the so-called persistence of the system and, therefore, does not imply global asymptotic stability. It is found that an orbitally asymptotically stable periodic orbit exists in that model. Some sufficient conditions which guarantee the global stability of positive equilibrium are given.

Key Words: global stability; predator–prey system; competitive systems; delay.

1. INTRODUCTION

The study of predator–prey systems began with the early work of Lotka and Volteva, who treated the simplest cases. In recent years, to understand better the dynamical behavior of predator–prey systems, various complications have been included [5, 7, 9, 13]. One complication that is certainly present in some cases is that the per capita predator growth rate shall be a function of the ratio of prey to predator abundance, and so should be the so-called predator functional response (see below). A typical ratio-dependent-type functional response model can be expressed in the

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form

$$\dot{N}(t) = rN(t)\left(1 - \frac{N(t)}{K}\right) - \frac{aN(t)P(t)}{mP(t) + N(t)},$$
$$\dot{P}(t) = -dP(t) + \frac{laN(t)P(t)}{mP(t) + N(t)}, \tag{1.1}$$

where $N(t)$ and $P(t)$ stand for prey and predator density, respectively. r, K, a, m, l, and d are positive constants that stand for prey intrinsic growth rate, carrying capacity, capturing rate, half capturing saturation constant, conversion rate, and predator death rate, respectively. System (1.1) was systematically studied by Kuang and Beretta [9] and Arditi and co-workers [1–3]. They discussed global stability of the boundary equilibria, positive equilibrium, and permanence of the system. Moreover, when the system is not persistent and positive equilibrium is unstable, they found that a periodic solution may occur. Their results included that the permanence of system (1.1) implies the global stability of positive equilibrium.

In this paper, we will consider a ratio-dependent-type predator–prey model with delay, which is described by the integro-differential system

$$\dot{N}(t) = rN(t)\left(1 - \frac{N(t)}{K}\right) - \frac{aN(t)P(t)}{mP(t) + N(t)},$$
$$\dot{P}(t) = -dP(t) + b\int_{-\infty}^{t} \frac{\delta N(\tau)P(\tau)}{mP(\tau) + N(\tau)} \exp(-\delta(t - \tau))\, d\tau, \tag{1.2}$$

where the exponential weight function satisfies

$$\int_{-\infty}^{t} \delta \exp(-\delta(t - \tau))\, d\tau = \int_{0}^{\infty} \delta \exp(-\delta s)\, ds = 1.$$

We are assuming in a more realistic fashion that the present level of the predator affects instantaneously the growth of the prey, but that the growth of the predator is influenced by the amount of prey in the past. More precisely, the number of predators grows depending on the weight-averaged time of the Michaelis–Menten function of N over the past by means of the function $Q(t)$ given by the integral

$$Q(t) \triangleq \int_{-\infty}^{t} \frac{\delta N(\tau)P(\tau)}{mP(\tau) + N(\tau)} \exp(-\delta(t - \tau))\, d\tau. \tag{1.3}$$

Clearly, this assumption implies that the influence of the past fades away exponentially and the number $1/\delta$ might be interpreted as the measure of the influence of the past. So, the smaller the $\delta > 0$, the longer the interval in the past in which the values of N are taken into account [4, 6, 11].

The integro-differential system (1.2) can be transformed [6, 11] into the system of differential equations on the interval $[0, \infty)$

$$\begin{aligned} \dot{N}(t) &= rN(t)\left(1 - \frac{N(t)}{K}\right) - \frac{aN(t)P(t)}{mP(t) + N(t)}, \\ \dot{Q}(t) &= \frac{\delta N(t)P(t)}{mP(t) + N(T)} - \delta Q(t), \\ \dot{P}(t) &= -dP(t) + bQ(t). \end{aligned} \tag{1.4}$$

We understand the relationship between the two systems as follows: If (N, P): $[0, \infty) \to R^2$ is the solution of (1.2) corresponding to continuous and bounded initial function $(\overline{N}, \overline{P})$: $(\infty, 0] \to R^2$, then (N, Q, P): $[o, \infty) \to R^3$ is a solution of (1.4) with $N(0) = \overline{N}(0)$, $P(0) = \overline{P}(0)$, and

$$Q(0) = \int_{-\infty}^{0} \frac{\delta \overline{N}(\tau)\overline{P}(\tau)}{m\overline{P}(\tau) + \overline{N}(\tau)} \exp(\delta\tau)\, d\tau.$$

Conversely, if (N, Q, P) is any solution of (1.4) defined on the entire real line and bounded on $(-\infty, 0]$, then Q is given by (1.3), and so (N, P) satisfies (1.2).

The objective of this paper is to perform a global qualitative study on system (1.4). Specifically, we shall show that ratio-dependent predator–prey models are rich in boundary dynamics. We also show that if the positive equilibrium is unstable, an orbitally asymptotically stable periodic solution exists. If the positive equilibrium is locally asymptotically stable, we prove that it is globally asymptotically stable by using the theory of competitive systems, compound matrices, and stability of periodic orbits. This is the same method elegantly applied by Li and Muldowney [10].

2. RICH BOUNDARY DYNAMICS AND PERMANENCE

In this section, we shall present some preliminary results, including the boundedness of solutions, permanence, and boundary dynamics for system (1.4). We shall point out here that, although (0, 0, 0) is defined for system (1.4), it cannot be linearized. So, the local stability of (0, 0, 0) cannot be studied. Indeed, this singularity at the origin, while causing much difficulty in our analysis of the system, contributes significantly to the richness of dynamics of the model (see also [1–3, 9]).

For the sake of simplicity, we put in dimensionless form the model equations (1.4), i.e.,

$$x = \frac{N}{K}, \qquad y = \frac{Km^2bQ}{a}, \qquad z = KmP,$$

and then use as dimensionless time, $\bar{t} = at/m$. This leads to the dimensionless equations (substituting t for $\bar{t}$)

$$\begin{aligned}
\dot{x}(t) &= \alpha x(t)(1 - x(t)) - \frac{x(t)z(t)}{z(t) + x(t)}, \\
\dot{y}(t) &= \beta \frac{x(t)z(t)}{z(t) + x(t)} - d_1 y(t), \\
\dot{z}(t) &= y(t) - d_2 z(t),
\end{aligned} \tag{2.1}$$

where

$$\alpha = \frac{mr}{a}, \qquad \beta = \frac{\delta m^3 b}{a^3}, \qquad d_1 = \frac{\delta m}{a}, \qquad d_2 = \frac{dm}{a}$$

are the dimensionless parameters. The initial condition for Eq. (2.1) may be any point in the nonnegative orthant of R^3_+ of R^3, where by R^3_+ we mean

$$R^3_+\{(x, y, z) \in R^3 : x \geq 0, \;\; y \geq 0, \;\; z \geq 0\}.$$

System (2.1) always has equilibria $E_0 = (0, 0, 0)$ and $E_1 = (1, 0, 0)$ and has a unique positive equilibrium $E^* = (x^*, y^*, z^*)$ if and only if any one of the following two conditions is true:

$$\begin{aligned}
&\text{(i) } 0 < \beta - d_1 d_2 < \alpha\beta, && \text{when } \alpha < 1, \\
&\text{(ii) } \beta - d_1 d_2 > 0, && \text{when } \alpha \geq 1.
\end{aligned} \tag{2.2}$$

In both cases, we have

$$x^* = \frac{(\alpha - 1)\beta + d_1 d_2}{\alpha\beta}, \qquad y^* = d_2 z^*, \qquad z^* = \frac{\beta - d_1 d_2}{d_1 d_2} x^*. \tag{2.3}$$

The Jacobian matrix $J_{E_1} = J(1, 0, 0)$ of system (2.1) at E_1 takes the form of

$$\begin{pmatrix} -\alpha & 0 & -1 \\ 0 & -d_1 & \beta \\ 0 & 1 & -d_2 \end{pmatrix}.$$

Clearly, whenever the positive steady state E^* exists, $(1, 0, 0)$ is unstable.

The Jacobian matrix $J^* = J(x^*, y^*, z^*)$ of system (2.1) at E^* takes the form of

$$\begin{pmatrix} \alpha - 2\alpha x^* - \left(\dfrac{z^*}{x^* + z^*}\right)^2 & 0 & -\left(\dfrac{x^*}{x^* + z^*}\right)^2 \\ \beta\left(\dfrac{z^*}{x^* + z^*}\right)^2 & -d_1 & \beta\left(\dfrac{x^*}{x^* + z^*}\right)^2 \\ 0 & 1 & -d_2 \end{pmatrix}. \tag{2.4}$$

The eigenvalue problem for the Jacobian matrix (2.4) provides the characteristic equation

$$\lambda^3 + Q_1\lambda^2 + Q_2\lambda + Q_3 = 0, \tag{2.5}$$

where the coefficients Q_i, $i = 1, 2, 3$, are

$$Q_1 = d_1 + d_2 + (\alpha - 1) + \left(\frac{d_1 d_2}{\beta}\right)^2,$$

$$Q_2 = (d_1 + d_2)\left[-\alpha + 2\alpha x^* + \left(\frac{z^*}{x^* + z^*}\right)^2\right] + d_1 d_2 - \beta\left(\frac{x^*}{x^* + z^*}\right)^2,$$

$$Q_3 = \frac{\alpha d_1 d_2}{\beta}(\beta - d_1 d_2)x^*.$$

Note that $Q_1 > 0$ and $Q_3 > 0$ if $\alpha \geq 1$ and $\beta > d_1 d_2$; that is, (ii) of (2.2) holds true. Furthermore,

$$\begin{aligned}\Delta &= Q_1 Q_2 - Q_3\\ &= \frac{d_1 + d_2}{\beta^4}\big[\big(\beta^2(\alpha - 1) + (d_1 d_2)^2\big)^2 + \beta^2(d_1 + d_2)\big(\beta^2(\alpha - 1) + (d_1 d_2)^2\big)\\ &\qquad + \beta^3 d_1 d_2(\beta - d_1 d_2)\big] - \frac{(d_1 d_2)^2}{\beta^3}(\beta - d_1 d_2)^2.\end{aligned}$$

By the Routh–Hurwitz criterion, we know that E^* is locally asymptotically stable if (ii) of (2.2) holds true and

$$\begin{aligned}(d_1 + d_2)\big[\big(\beta^2(\alpha - 1) + (d_1 d_2)^2\big)^2 + \beta^2(d_1 + d_2)\big(\beta^2(\alpha - 1) + (d_1 d_2)^2\big)\\ + \beta^3 d_1 d_2(\beta - d_1 d_2)\big] > \beta(d_1 d_2(\beta - d_1 d_2))^2.\end{aligned} \tag{2.6}$$

Standard and simple arguments show that solutions of the system (2.1) always exist and stay positive. Indeed, as is obvious for system (2.1), we have

$$\lim_{t\to+\infty} \sup x(t) \leq 1.$$

Then there is a $T > 0$ such that for any sufficiently small $\epsilon > 0$ we have

$$x(t) \leq 1 + \epsilon \qquad \text{for } t > T.$$

THEOREM 2.1. *There is an $M > 0$ such that, for any positive solution $(x(t), y(t), z(t))$ of system* (2.1),

$$y(t) < M,\ z(t) < M \qquad \textit{for all large } t.$$

Proof. Set

$$V = \beta x(t) + y(t).$$

Calculating the derivative of V along the solutions of system (2.1), we find

$$\begin{aligned} \dot{V}(t) &= \alpha\beta x(1-x) - d_1 y_1 \\ &= -d_1 V + (d_1\beta + \alpha\beta)x - \alpha\beta x^2 \\ &\leq -d_1 V + M_0, \end{aligned}$$

where $M_0 = \beta(d_1+\alpha)^2/4\alpha$. Recall that $x(t) \leq 1+\epsilon$ for all $t > T$. Then there exists an M_1, depending only on the parameters of system (2.1), such that $V(t) < M_1$ for $t > T$. Then $y(t)$ has an ultimately above bound. It follows from the third equation of Eq. (2.1) that $z(t)$ has an ultimately above bound, say, their maximum is an M. Then the assertion of Theorem 2.1 now follows and the proof is complete. This shows that system (2.1) is dissipative. ∎

Define

$$\Omega = \{(x, y, z) : 0 \leq x \leq 1,\ 0 \leq y,\ z \leq M\}.$$

It is easy to see that, for system (2.1), if $\alpha > 1$, then

$$\dot{x} > x(\alpha - 1 - \alpha x), \tag{2.7}$$

which implies that $\lim_{t\to+\infty} \inf x(t) \geq (\alpha-1)/\alpha \stackrel{\triangle}{=} \underline{x}$. Hence there is a $T > 0$ such that $x(t) > \underline{x}/2$, for $t > T$, and we have

$$\begin{aligned} \dot{y} &\geq \beta\frac{z\underline{x}/2}{\underline{x}/2+z} - d_1 y, \\ \dot{z} &= y - d_2 z. \end{aligned} \tag{2.8}$$

Now, we consider the comparison equations

$$\begin{aligned} \dot{u} &= \beta\frac{v\underline{x}/2}{\underline{x}/2+v} - d_1 u, \\ \dot{v} &= u - d_2 v. \end{aligned} \tag{2.9}$$

Obviously, if $\beta > d_1 d_2$, then the unique positive equilibrium (u^*, v^*) of Eq. (2.9), where $u^* = d_2 v^*,\ v^* = \underline{x}(\beta - d_1 d_2)/2d_1 d_2$, exists and is locally asymptotically stable. Let $0 < u(t_0) < y(t_0)$, $0 < v(t_0) < z(t_0)$, $t_0 > T$. If $(u(t), v(t))$ is a solution of Eq. (2.9) with initial conditions $(u(t_0), v(t_0))$ for $t_0 > T$, then $y(t) \geq u(t)$, $z(t) \geq v(t)$ for $t > t_0$. If for Eq. (2.9) there exists a solution which is unbounded, say $(\bar{u}(t), v(t)) \to (+\infty, +\infty)$, as

$t \to +\infty$, then it follows that for Eq. (2.1) there exists at least one solution, say, $(x(t), y(t), z(t))$, which is also unbounded provided there is a satisfying initial condition $0 < \bar{u}(t_0) < y(t_0)$, $0 < \bar{v}(t_0) < z(t_0)$. This contradicts the boundedness of solutions of Eq. (2.1). Hence we must have that all the solutions of Eq. (2.9) are bounded, it follows that the unique positive equilibrium (u^*, v^*) is globally asymptotically stable. Hence we have

$$\lim_{t\to+\infty} \inf y(t) \geq u^* \triangleq \underline{y}, \qquad \lim_{t\to+\infty} \inf z(t) \geq v^* \triangleq \underline{z}.$$

Theorem 2.1 and the above arguments imply that.

THEOREM 2.2. *If $\alpha > 1$ and $\beta > d_1 d_2$, then system* (2.1) *is permanent.*

Assume below that $\alpha + d_2 < 1$ in system (2.1). Then there is a $\xi > 0$ such that $1/(1+\xi) = \alpha + d_2$. Let $\delta_1 = x(0)/z(0) < \xi$. We claim that, for all $t > 0$, $x(t)/z(t) < \xi$ and $\lim_{t\to+\infty} x(t) = 0$. Otherwise, there is a first time t_1, $x(t_1)/z(t_1) = \xi$, and, for $t \in [0, t_1)$, $x(t)/z(t) < \xi$. Then, for $t \in [0, t_1]$, we have

$$\dot{x}(t) \leq \alpha x - \frac{x}{1 + x/z} \leq x\left[\alpha - \frac{1}{1+\xi}\right],$$

which implies that $x(t) \leq x(0)e^{-d_2 t}$. However, for all $t \geq 0$,

$$\dot{z}(t) \geq -d_2 z(t),$$

which implies that $z(t) \geq z(0)e^{-d_2 t}$. This shows that, for $t \in [0, t_1]$,

$$\frac{x(t)}{z(t)} \leq \frac{x(0)}{z(0)} = \delta_1 < \xi,$$

a contradiction to the existence of t_1, proving the claim. This in turn implies that $x(t) \leq x(0)e^{-d_2 t}$ for all $t \geq 0$. That is, $\lim_{t\to+\infty} x(t) = 0$. Hence we have established the following result (recall that system (2.1) is not persistent if $\min\{\lim_{t\to+\infty} \inf x(t), \lim_{t\to+\infty} \inf y(t), \lim_{t\to+\infty} \inf z(t)\} = 0$ for some of its positive solutions):

THEOREM 2.3. *If $\alpha + d_2 < 1$, then system* (2.1) *is not persistent.*

Note that, under the assumption $\alpha + d_2 < 1$, system (2.1) may have positive steady state. This shows that system (2.1) can have both positive steady state and positive solutions that tend to the boundary. In fact, we also have

THEOREM 2.4. *If $\alpha + d_2 < 1$, then there exist positive solutions $(x(t), y(t), z(t))$ of system* (2.1) *such that* $\lim_{t\to+\infty}(x(t), y(t), z(t)) = (0, 0, 0)$.

Proof. The argument leading to Theorem 2.3 shows that $\lim_{t\to+\infty} x(t) = 0$, and, for $t \geq 0$, $x(t)/z(t) \leq \delta_1$, provided that $\delta_1 = x(0)/z(0) < \xi$, where $\xi = 1/(\alpha + d_2) - 1$. Let $(x(t), y(t), z(t))$ be the solution of Eq. (2.1) with $x(0)/z(0) < \xi$. Since the solution $(x(t), y(t), z(t))$ of Eq. (2.1) is bounded, we have

$$0 \leq \overline{l_1} \triangleq \lim_{t\to+\infty} \sup y(t) < \infty, \qquad 0 \leq \overline{l_2} \triangleq \lim_{t\to+\infty} \sup z(t) < +\infty.$$

Since $\lim_{t\to+\infty} x(t) = 0$, there is a t_1 such that, for $t > t_1$, $x(t) \leq d_1\overline{l_1}/2\beta$. If $\overline{l_1} > 0$, then there is a $t_2 > t_1$ such that $y(t_2) > \overline{l_1}/2$ and $\dot{y}(t_2) > 0$. Moreover,

$$\dot{y}(t) \leq \beta x(t) - d_1 y(t).$$

Hence

$$0 < \dot{y}(t_2) \leq \beta x(t_2) - d_1 y(t_2).$$

Then

$$x(t_2) > \frac{d_1\overline{l_1}}{2\beta}.$$

This is a contradiction to $x(t) \leq d_1\overline{l_1}/2\beta$ for $t > t_1$. Hence we must have $\overline{l_1} = 0$. Incorporating into the positivity of solutions, we have $\lim_{t\to+\infty} y(t) = 0$. It follows that $\lim_{t\to+\infty} z(t) = 0$. This completes the proof. ∎

Theorem 2.4 implies that, if $\alpha + d_2 < 1$, then the boundary equilibrium $(1, 0, 0)$ of system (2.1) is not globally asymptotically stable. Note that, under the condition $\alpha + d_1 < 1$, system (2.1) can have no positive steady state and at the same time $(1, 0, 0)$ is locally stable (just add the assumption $\beta < d_1 d_2$). In this case, some solutions tend to $(1, 0, 0)$ and some tend to $(0, 0, 0)$. Hence the above theorem shows that system (2.1) can have bistability.

THEOREM 2.5. *If* $\alpha \geq 1$ *and* $\beta \leq d_1 d_2$, *then* $(1, 0, 0)$ *is globally asymptotically stable.*

Proof. From the last two equations of Eq. (2.1), we have

$$\begin{aligned} \dot{y}(t) &\leq \beta z(t) - d_1 y(t), \\ \dot{z}(t) &= y(t) - d_2 z(t). \end{aligned} \tag{2.10}$$

We consider the comparison equations

$$\begin{aligned} \dot{u}(t) &= \beta v(t) - d_1 u(t), \\ \dot{v}(t) &= u(t) - d_2 v(t). \end{aligned} \tag{2.11}$$

It is easy to show that if $\beta \le d_1 d_2$ for any solution of (2.11) with non-negative initial values we have $\lim_{t\to+\infty} u(t) = 0$, $\lim_{t\to+\infty} v(t) = 0$. Let $0 < y(0) \le u(0)$, $0 < z(0) \le v(0)$. If $(u(t), v(t))$ is a solution of system (2.11) with initial value $(u(0), v(0))$, then by the comparison theorem we have $y(t) \le u(t)$, $z(t) \le v(t)$ for all $t > 0$. Hence $\lim_{t\to+\infty} y(t) = 0$ and $\lim_{t\to+\infty} z(t) = 0$. Moreover, $\lim_{t\to+\infty} \inf x(t) \ge \underline{x}$, $\underline{x} \triangleq (\alpha - 1)/\alpha$.

Assume first that $\alpha > 1$. Then, for an $\epsilon \in (0, 1)$, there exists $T = T(\epsilon)$ such that, for $t > T$,

$$\alpha x(t)(1 - \epsilon - x(t)) \le \dot{x}(t) \le \alpha x(t)(1 - x(t)).$$

This clearly shows that $\lim_{t\to+\infty} x(t) = 1$.

Assume now that $\alpha = 1$. Then

$$\dot{x}(t) = x(1 - x) - \frac{xz}{x + z} = \frac{x^2}{x + z}(1 - x - z).$$

Since $\lim_{t\to+\infty} z(t) = 0$, we see that (by a standard comparison argument)

$$\lim_{t\to+\infty} x(t) = 1.$$

This proves the theorem. ∎

3. MAIN FACTS ON THREE-DIMENSIONAL COMPETITIVE SYSTEMS

In this section, we will summarize the main facts related to our research. Let us consider the system of differential equations

$$\dot{X} = F(X), \qquad X \in D, \tag{3.1}$$

where D is an open subset on R^3 and F is twice continuously differentiable in D. The noncontinuable solution of (3.1) satisfying $X(0) = X_0$ is denoted by $X(t, X_0)$, the positive (negative) semi-orbit through X_0 is denoted by $\phi^+(X_0)(\phi^-(X_0))$, and the orbit through X_0 is denoted by $\phi(0) = \phi^-(X_0) \cup \phi^+(X_0)$. We use the notation $\omega(X_0)(\alpha(X_0))$ for the positive (negative) limit set of $\phi^+(X_0)$ $(\phi^-(X_0))$, provided the latter semi-orbit has compact closure in D.

System (3.1) is *competitive* in D [8, 14–16] if, for some diagonal matrix $H = \operatorname{diag}(\epsilon_1, \epsilon_2, \epsilon_3)$, where ϵ_i is either 1 or -1, $H(DF(X))H$ has non-positive off-diagonal elements for $X \in D$, where $DF(X)$ is the Jacobian of Eq. (3.1). It is shown in [16] that if D is convex the flow of such a system preserves for $t < 0$ the partial order in R^3 defined by the orthant

$$K_1 = \{(X_1, X_2, X_3) \in R^3 : \epsilon_i X_i \ge 0\}.$$

Hirsch [8] and Smith [14, 16] proved that three-dimensional competitive systems that live in convex sets have the Poincare–Bendixson property [12]; that is, any nonempty compact omega limit set that contains no equilibria must be a closed orbit.

THEOREM 3.1. *Assume D is convex and bounded. Suppose system* (3.1) *is competitive and permanent and has the property of stability of periodic orbits. If $\bar{x}_0$ is the only equilibrium point in* int D *and if it is locally asymptotically stable, then it is globally asymptotically stable in* int D.

The following theorem is proved in [15].

THEOREM 3.2. *Let* (3.1) *be a competitive system in $D \subset R^3$ and suppose that D contains a unique equilibrium point X^* which is hyperbolic and assume that $DF(X^*)$ is irreducible. Suppose further that $W^s(X^*)$, the stable manifold of X^*, is one dimensional. If $q \in D \backslash W^s(X^*)$ and $\phi^+(q)$ has compact closure in D, then $\omega(q)$ is a nontrivial periodic orbit.*

The existence of an orbitally stable periodic solution can also be proved. We introduce the following hypotheses:

(H1) System (3.1) is dissipative: For each $X \in D$, $\phi^+(X)$ has compact closure in D. Moreover, there exists a compact subset B of D with property that for each $\overline{X} \in D$ there exists $T(\overline{X}) > 0$ such that $X(t, \overline{X}) \in B$ for $t \geq T(\overline{X})$.

(H2) System (3.1) is competitive and irreducible in D.

(H3) D is an open, p-convex subset of R^3.

(H4) D contains a unique equilibrium point X^* and $\det(DF(X^*)) < 0$.

The following result holds [14]:

THEOREM 3.3. *Let* (H1)–(H4) *hold. Then either*

(a) *X^* is stable or*

(b) *there exists a nontrivial orbitally stable periodic orbit in D. In addition, let us assume that F is analytic in D. If X^* is unstable, then there is at least one but no more than finitely many periodic orbits for* (3.1) *and at least one of these is orbitally asymptotically stable.*

By looking at its Jacobian matrix and choosing the matrix H as

$$H = \begin{pmatrix} 1 & 0 & 0 \\ 0 & -1 & 0 \\ 0 & 0 & 1 \end{pmatrix},$$

we can see that system (2.1) is competitive in Ω, with respect to the partial order defined by the orthant $K_1 = \{(x, y, z) \in R^3 : x \geq 0, y \leq 0, z \geq 0\}$. Our main results will follow from this observation and the above theorems.

4. GLOBAL STABILITY OF POSITIVE EQUILIBRIUM

This section is devoted to an investigation of the global stability of the positive equilibrium E^*.

THEOREM 4.1. *Let* $\alpha > 1$ *and* $\beta > d_1 d_2$ *and let* (2.6) *hold. Then the positive equilibrium* E^* *of Eq.* (2.1) *is globally asymptotically stable provided one of the following two assumption holds*:

(H5) $\alpha < d_1$ *and* $\underline{x} \geq 1/2$.

(H6) $\alpha < d_1$ *and* $\underline{x} > \alpha + d_1/2\alpha$.

The proof of this theorem is the same as those of Theorems 2.1 and 4.2 in 8. Since system (2.1) is competitive, permanent if $\alpha > 1,\ \beta > d_1 d_2$, and E^* is locally asymptotically stable if (2.6) holds true. Furthermore, in accordance with Theorem 3.1 (where we can choose $D = \Omega$), Theorem 4.1 would be established if we show that system (2.1) has the property of stability of periodic orbits. In the following, we prove it.

PROPOSITION 4.1. *Assume condition* (H5) *or* (H6) *holds true. Then system* (2.1) *has the property of stability of periodic orbits.*

Proof. Let $p(t) = (x(t), y(t), z(t))$ be a periodic solution whose orbit Γ is contained in int Ω. In accordance with the criterion given by Muldowney in [12], for the asymptotic orbital stability of a periodic orbit of a general autonomous system, it is sufficient to prove that the linear nonautonomous system

$$\dot{W}(t) = (DF^{[2]}(p(t)))W(t) \tag{4.1}$$

is asymptotically stable, where $DF^{[2]}$ is the second additive compound matrix of the Jacobian DF (see the Appendix).

The Jacobian of Eq. (2.1) is given by

$$DF = \begin{pmatrix} \alpha - 2\alpha x - \left(\dfrac{z}{A}\right)^2 & 0 & -\left(\dfrac{x}{A}\right)^2 \\ \beta\left(\dfrac{z}{A}\right)^2 & -d_1 & \beta\left(\dfrac{x}{A}\right)^2 \\ 0 & 1 & -d_2 \end{pmatrix},$$

where $A = x + z$. For the solution $p(t)$. Eq. (4.1) becomes

$$\begin{aligned} \dot{w}_1 &= -\left(-\alpha + 2\alpha x + \frac{z^2}{A^2} + d_1\right)w_1 + \frac{\beta x^2}{A^2}w_2 + \frac{x^2}{A^2}w_3, \\ \dot{w}_2 &= w_1 + \left(\alpha - 2\alpha x - \frac{z^2}{A^2} - d_2\right)w_2, \\ \dot{w}_3 &= \frac{\beta z^2}{A^2}w_2 - (d_1 + d_2)w_3. \end{aligned} \tag{4.2}$$

To prove that Eq. (4.2) is asymptotically stable, we shall use the following Lyapunov function, which is similar to the one found in [10] for the SEIR model,

$$V(w_1(t), w_2(t), w_3(t), x(t), y(t), z(t)) = \left\| \left(w_1(t), \frac{y(t)}{z(t)} w_2(t), \frac{y(t)}{\beta z(t)} w_3(t) \right) \right\|,$$

where $\|\cdot\|$ is the norm in R^3 defined by

$$\|(w_1, w_2, w_3)\| = \sup\{|w_1|, |w_2| + |w_3|\}.$$

From Theorem 2.2, we obtain that the orbit of $p(t)$ remains at a positive distance from the boundary of Ω. Therefore

$$y(t) \geq \eta, \ z(t) \geq \eta, \ \eta = \min\{\underline{y}, \underline{z}\} \qquad \text{for all large } t.$$

Hence the function V is well defined along $p(t)$ and

$$V(w_1, w_2, w_3; x, y, z) \geq \frac{\eta}{M} \|(w_1, w_2, w_3)\|. \tag{4.3}$$

Along a solution $(w_1(t), w_2(t), w_3(t))$ of the system (4.2), V becomes

$$V(t) = \sup\left\{ |w_1(t)|, \frac{y(t)}{z(t)} \left(|w_2(t)| + \frac{|w_3(t)|}{\beta} \right) \right\}.$$

Then we have the following inequalities:

$$\begin{aligned} D_+|w_1(t)| &\leq -\left(-\alpha + 2\alpha x + \frac{z^2}{A^2} + d_1 \right) |w_1(t)| \\ &\quad + \frac{\beta x^2}{A^2} \left(|w_2(t)| + \frac{|w_3(t)|}{\beta} \right) \\ &\leq -\left(-\alpha + 2\alpha x + \frac{z^2}{A^2} + d_1 \right) |w_1(t)| \\ &\quad + \frac{\beta x^2 z}{A^2 y} \left(\frac{y}{z} \left(|w_2(t)| + \frac{|w_3(t)|}{\beta} \right) \right), \end{aligned} \tag{4.4}$$

$$D_+|w_2(t)| \leq -\left(-\alpha + 2\alpha x + \frac{z^2}{A^2} + d_2 \right) |w_2(t)| + |w_1(t)|, \tag{4.5}$$

$$D_+|w_3(t)| \leq -(d_1 + d_2)|w_3(t)| + \frac{\beta z^2}{A^2} |w_2(t)|. \tag{4.6}$$

From (4.5) and (4.6), we get

$$D_+\left(|w_2(t)| + \frac{|w_3(t)|}{\beta} \right) \leq |w_1(t)| - G\left(|w_2(t)| + \frac{|w_3(t)|}{\beta} \right),$$

where $G = \min\{-\alpha + 2\alpha x + d_2, d_1 + d_2\}$. Therefore

$$
\begin{aligned}
&D_+\left(\frac{y}{z}\left(|w_2(t)| + \frac{|w_3(t)|}{\beta}\right)\right)\\
&\quad = \left(\frac{\dot{y}}{y} - \frac{\dot{z}}{z}\right)\frac{y}{z}\left(|w_2(t)| + \frac{|w_3(t)|}{\beta}\right) + \frac{y}{z}D_+\left(|w_2(t)| + \frac{|w_3(t)|}{\beta}\right)\\
&\quad \le \left(\frac{\dot{y}}{y} - \frac{\dot{z}}{z}\right)\frac{y}{z}\left(|w_2(t)| + \frac{|w_3(t)|}{\beta}\right) + \frac{y}{z}|w_1(t)|G\frac{y}{z}\left(|w_2(t)| + \frac{|w_3(t)|}{\beta}\right)\\
&\quad \le \frac{y}{z}|w_1(t)| + \left(\frac{\dot{y}}{y} - \frac{\dot{z}}{z} - G\right)\frac{y}{z}\left(|w_2(t)| + \frac{|w_3(t)|}{\beta}\right).
\end{aligned}
\tag{4.7}
$$

From (4.4) and (4.7), we get

$$
D_+V(t) \le \sup\{h_1(t), h_2(t)\}V(t), \tag{4.8}
$$

where

$$
\begin{aligned}
h_1(t) &= -\left(-\alpha + 2\alpha x + \frac{z^2}{A^2} + d_1\right) + \frac{\beta x^2 z}{A^2 y},\\
h_2(t) &= \frac{y}{z} + \frac{\dot{y}}{y} - \frac{\dot{z}}{z} - G.
\end{aligned}
$$

From the last two equations of system (2.1), we have

$$
\begin{aligned}
h_1(t) &\le -\left(-\alpha + 2\alpha x + \frac{z^2}{A^2} + d_1\right) + \frac{\beta x z}{A y}\\
&= \alpha - 2\alpha x - \frac{z^2}{A^2} - d_1 + \frac{\dot{y}}{y} + d_1\\
&= \alpha - 2\alpha x - \frac{z^2}{A^2} + \frac{\dot{y}}{y}.
\end{aligned}
$$

If (H5) holds true, then $-d_1 < \alpha - 2\alpha x < 0$, that is, $G = -\alpha + 2\alpha x + d_2$. Then we get

$$
\begin{aligned}
h_2(t) &= \frac{y}{z} + \frac{\dot{y}}{y} - \frac{\dot{z}}{z} - (-\alpha + 2\alpha x + d_2)\\
&= \frac{\dot{y}}{y} + \alpha - 2\alpha x.
\end{aligned}
$$

Hence

$$
\sup\{h_1(t), h_2(t)\} \le \frac{\dot{y}}{y} + \alpha - 2\alpha x \le -\mu + \frac{\dot{y}}{y}, \tag{4.9}
$$

where $\mu > 0$ such that $\alpha - 2\alpha x \le -\mu < 0$.

If (H6) holds true, then $\alpha - 2\alpha x < -d_1$, that is, $G = d_1 + d_2$. Then we get

$$h_2(t) = \frac{y}{z} + \frac{\dot{y}}{y} - \frac{\dot{z}}{z} - (d_1 + d_2) = -d_1 + \frac{\dot{y}}{y}.$$

Hence

$$\sup\{h_1(t), h_2(t)\} \le -d_1 + \frac{\dot{y}}{y}. \tag{4.10}$$

Let $\bar{\mu} = \min\{\mu, d_1\}$. Then, from (4.9) and (4.10), we have

$$\sup\{h_1(t), h_2(t)\} \le -\bar{\mu} + \frac{\dot{y}}{y}. \tag{4.11}$$

Therefore, from (4.8) and Gronwall's inequality, we obtain

$$V(t) \le V(0)y(t)e^{-\bar{\mu}t} \le V(0)Me^{-\bar{\mu}t},$$

which implies that $V(t) \to 0$ as $t \to +\infty$. By (4.3) it turns out that

$$(w_1(t), w_2(t), w_3(t)) \to 0 \qquad \text{as } t \to +\infty.$$

This implies that the linear system Eq. (4.2) is asymptotically stable and therefore the periodic solution is asymptotically orbitally stable. This proves Proposition 4.1. ∎

As noted before, this result proves Theorem 4.1.

5. EXISTENCE OF A STABLE PERIODIC ORBIT

Out main result below gives sufficient conditions that almost every solution is asymptotically periodic.

THEOREM 5.1. *Let $\alpha > 1$ and $\beta > d_1 d_2$. Then positive equilibrium is locally asymptotically stable if* (2.6) *holds. There exists a one-dimensional stable manifold $W^s(E^*)$ if* (2.6) *is reversed. Furthermore, there exists an orbitally asymptotically stable periodic orbit, and the omega limit set of every solution $(x(t), y(t), z(t))$ with $x(0) > 0, y(0) > 0, z(0) > 0$ and $(x(0), y(0), z(0)) \notin W^s(E^*)$ is a nonconstant periodic orbit.*

Proof. It suffices to prove the second assumption of Theorem 5.1. We apply Theorems 3.2 and 3.3 to the following transform system. A change of variables $w_1 = -x$, $w_2 = y$, $w_3 = -z$ transforms system (2.1) into

$$\begin{aligned} \dot{w}_1 &= \alpha w_1(1 + w_1) - \frac{w_1 w_3}{w_1 + w_3}, \\ \dot{w}_2 &= -\beta \frac{w_1 w_3}{w_1 + w_3} - d_1 w_2, \\ \dot{w}_3 &= -w_2 - d_2 w_3. \end{aligned} \tag{5.1}$$

If we write (5.1) as $\dot{w} = f(w)$, the Jacobian matrix of f at w is

$$J(w) = \begin{pmatrix} \alpha + 2\alpha w_1 - \left(\dfrac{w_3}{w_1 + w_3}\right)^2 & 0 & -\left(\dfrac{w_1}{w_1 + w_3}\right)^2 \\ -\beta\left(\dfrac{w_3}{w_1 + w_3}\right)^2 & -d_1 & -\beta\left(\dfrac{w_1}{w_1 + w_3}\right)^2 \\ 0 & -1 & -d_2 \end{pmatrix}.$$

$J(w)$ has nonpositive off-diagonal elements at each point of $D = \{(w_1, w_2, w_3) : w_1 < 0, w_2 > 0, w_3 < 0\}$. Let $w_1^* = -x^*, w_2^* = y^*, w_3^* = -z^*$. It is obvious that (w_1^*, w_2^*, w_3^*) is the unique equilibrium of Eq. (5.1). Since the inequality (2.6) is reversed, the analysis in Section 2 shows that (w_1^*, w_2^*, w_3^*) is unstable and $\det J(w^*) < 0$. Furthermore, we see that the stable manifold of E^* is one dimensional. The existence of an orbitally asymptotically stable periodic orbit follows from Theorem 3.3 and the analytically of the vector field. Moreover, since Eq. (2.1) is permanent, there exists a compact subset B of D such that, for each $w_0 \in D$, there exists a $T(w_0) > 0$ such that $w(t, w_0) \in B$ for all $t \geq T(w_0)$. Note that (H1)–(H4) hold and using Theorems 3.2 and 3.3 implies the final assertion. ∎

6. DISCUSSION

In this paper, a ratio-dependent predator–prey model with time lag for predator is proposed and investigated. We show that a ratio-dependent predator–prey model with delay is rich in boundary dynamics; specifically, system (2.1) can have both positive steady state (or periodic solution) and positive solutions that tend to the origin. Using results about competitive systems, we prove that there exists an orbitally asymptotically stable periodic orbit when system (2.1) is permanent and the positive equilibrium is unstable. Comparing our results with the results of Kuang and Beretta [9], we know that this is a new phenomenon, and this shows that the time lag may be the cause of periodic oscillations in the populations. Incorporating our results into the compound matrices and stability of the periodic orbit, we show that unique positive equilibrium is globally asymptotically stable.

In the following, we classify the parameter region to state the dynamical behavior of the solutions and make some computer simulations, and therefore show the difference between our results and those obtained in [9].

(1) $\alpha > 1$, $\beta - d_1 d_2 > 0$. Theorem 2.2 states that system (2.1) is permanent and the unique positive equilibrium E^* exists. If (2.6) holds true, E^* is locally asymptotically stable and further E^* is globally asymptotically

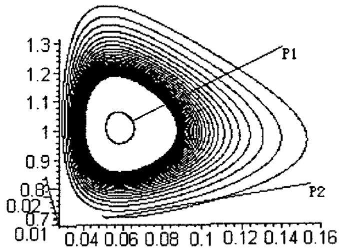

FIG. 1. $\alpha = 1.0005$, $\beta = 1/180$, $d_1 = 1/50$, $d_2 = 1/60$. Initial value P_1: $x(0) = 0.06$, $y(0) = 0.015$, $z(0) = 0.9$. Initial value P_2: $x(0) = 0.05$, $y(0) = 0.01$, $z(0) = 0.7$.

stable provided (H5) or (H6) holds. Note that it is easy to choose parameters such that the conditions of Theorem 4.1 are satisfied. For example, we can choose $d_1 = 1/30$, $d_2 = 1/40$, $\alpha = 2.3$, $\beta = 1/20$. Then the positive equilibrium is globally asymptotically stable. If (2.6) is reversed, then E^* is unstable and an orbitally asymptotically stable periodic solution exists (see Fig. 1). However, in this case, Kuang and Beretta [9] proved that positive equilibrium is globally asymptotically stable for system (1.1).

(2) $\alpha \geq 1$, $\beta - d_1 d_2 \leq 0$. Theorem 2.5 shows that $E_1 = (1, 0, 0)$ is globally asymptotically stable.

(3) $\alpha < 1, \alpha + d_2 \geq 1, 0 < \beta - d_1 d_2 < \alpha\beta$. In this case, positive equilibrium E^* also exists. Figure 2 shows that a small-amplitude periodic solution may exist as well as an asymptotically stable origin. In this case, however, Kuang and Beretta [9] found that no periodic solution occurs and E^* is locally asymptotically stable.

(4) $\alpha + d_2 < 1, 0 < \beta - d_1 d_2 < \alpha\beta$. Theorem 2.3 shows that system (2.1) is not persistent but E^* exists. In this case, we obtain the phenomenon which is similar to Fig. 2 and the results [9].

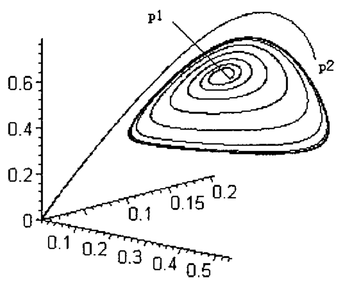

FIG. 2. $\alpha = 0.92$, $\beta = 1/30$, $d_1 = 1/30$, $d_2 = 1/4$. Initial value P_1: $x(0) = 0.2047$, $y(0) = 0.1385$, $z(0) = 0.5443$. Initial value P_2: $x(0) = 0.3$, $y(0) = 0.2$, $z(0) = 0.6$.

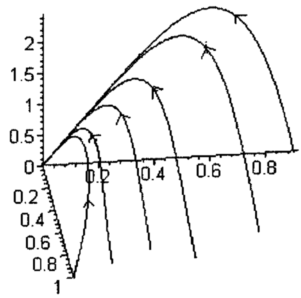

FIG. 3. $\alpha = 0.7$, $\beta = 1/20$, $d_1 = 1/20$, $d_2 = 1/4$.

(5) $\alpha < 1$, $\beta - d_1 d_2 \geq \alpha\beta$. Although mathematically we cannot prove the stability of origin, computer simulation suggests that it is globally asymptotically stable (see Fig. 3).

There are still many interesting and challenging mathematical questions that need to be studied for system (2.1). For example, we cannot analyze system (2.1) in its all parameter regions; there is room for improvement. However, significant improvements appear to be difficult. Also, we are unable to show the stability of origin, or to show system (2.1) has a unique positive limit cycle, when E^* is unstable. We leave this for future work.

APPENDIX

In this appendix, we shall give the definition of an additive compound matrix. A survey of properties of additive compound matrices together with their connections to differential equations may be found in [10, 12].

We start by recalling the definition of a kth exterior power or multiplicative compound of a matrix.

DEFINITION A.1. Let A be an $n \times m$ matrix of real or complex numbers. Let $a_{i_1, \ldots, i_k, j_1, \ldots, j_k}$ be the minor of A determined by the rows $(i_1, \ldots, i_k)$ and the columns $(j_1, \ldots, j_k)$, $1 \leq i_1 < i_2 < \cdots < i_k \leq n$, $1 \leq j_1 < j_2 < \cdots < j_k \leq m$. The kth *multiplicative compound matrix* $A^{(k)}$ of A is the $\binom{n}{k} \times \binom{m}{k}$ matrix whose entries, written in lexicographic order, are $a_{i_1, \ldots, i_k, j_1, \ldots, j_k}$.

In particular, when A is an $n \times k$ matrix with columns $a_1, a_2, \ldots, a_k$, $A^{(k)}$ is the exterior product $a_1 \wedge a_2 \wedge \cdots \wedge a_k$.

In the case $m = n$, the additive compound matrices are defined in the following way.

DEFINITION A.2. Let A be an $n \times n$ matrix. The kth *additive compound* $A^{[k]}$ of A is the $\binom{n}{k} \times \binom{n}{k}$ matrix given by

$$A^{[k]} = D(I + hA)^{(k)}|_{h=0}, \tag{A.1}$$

where D denotes the derivative with respect to h.

If $B = A^{[k]}$, then the following formula for $b_{i,j}$ can be deduced from Eq. (A.1). For any integer $i = 1, \dots, \binom{n}{k}$, let $(i) = (i_1, i_2, \dots, i_k)$ be the ith member in the lexicographic ordering of all k-tuples of integers such that $1 \le i_1 < i_2 < \cdots < i_k \le n$. Then

$$b_{i,j} = \begin{cases} a_{i_1,i_1} + \cdots + a_{i_k,i+k} & \text{if } (i)=(j), \\ (-1)^{r+s} a_{i_s,j_r} & \text{if exactly one entry } i_s \text{ in } (i) \text{ does not occur} \\ & \quad \text{in } (j) \text{ and } j_r \text{ does not occur in } (i), \\ 0 & \text{if } (i) \text{ differs from } (j) \text{ in two or more entries.} \end{cases}$$

In the extreme cases when $k = 1$ and $k = n$, we have $A^{[1]} = A$ and $A^{[n]} = \mathrm{tr}(A)$. For $n = 3$, the matrices $A^{[k]}$ are as follows:

$$A^{[1]} = A, \qquad A^{[2]} = \begin{pmatrix} a_{11} + a_{22} & a_{23} & -a_{13} \\ a_{32} & a_{11} + a_{33} & a_{12} \\ -a_{31} & a_{21} & a_{22} + a_{33} \end{pmatrix},$$

$$A^{[3]} = a_{11} + a_{22} + a_{33}.$$

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